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## RESEARCH ARTICLE

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**Motor unit firing behavior in human arm flexor muscles during sinusoidal isometric contractions and movements**

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**Abstract** Simultaneous recordings of action potentials (APs) of multiple single motor units (MUs) were obtained in brachialis and biceps (caput breve) muscles during sinusoidally modulated isometric contractions of elbow flexor muscles and during sinusoidal flexion/extension movements in the elbow against a preload in the extension direction. The results show that MUs typically fire in one short burst for each sinusoidal cycle. The mean phase lead of the bursts of APs relative to a sinusoidally modulated isometric torque in the elbow joint or relative to sinusoidal movements in the elbow increases gradually with frequency. The increase of the mean phase lead during isometric contractions was very similar for all MUs and could be explained well by modeling the force production of MUs with a second-order linear low-pass system. For sinusoidal flexion/extension movements each MU reveals a specific, reproducible phase lead as a function of frequency. However, there is a large variability in phase behavior between MUs. Also, the modulation of the firing rate for sinusoidal isometric contractions versus sinusoidal movements appeared to be different for various MUs. In simultaneous recordings some MUs clearly revealed a larger firing rate in each burst for movements relative to isometric contractions, whereas other MUs revealed a smaller firing rate. This suggests that some MUs are preferentially activated during movements whereas others are preferably activated during isometric contractions. The results demonstrate task-dependent changes in the relative activation of MUs within a single muscle for sinusoidal isometric contractions and movements.

**Key words** Motor unit · Isometric tasks · Movements · Human

**Introduction**

There is an accumulation of evidence indicating that the relative activation of muscles acting across a joint depends on the particular motor task. For example, Smith et al. (1980) showed in cat that the lateral gastrocnemius muscle, which mainly contains fast-twitch motor units (MUs) with a relatively high isometric recruitment threshold (IRT), was active during rapid ankle extension movements in paw shakes, whereas the soleus muscle, which mainly consists of slow-twitch MUs with a low IRT, was not. Since soleus is usually active together with the gastrocnemius muscle, this result demonstrates a change in the relative activation of muscles for fast repetitive movements, which may have a functional significance considering the different contractile properties of the lateral gastrocnemius and the soleus muscles. Other evidence for a task-dependent activation of muscles was presented by Theeuwen et al. (1994) who showed that the electromyographic (EMG) activity in elbow flexor muscles in man was distributed differently in isometric contractions and in movements. In addition, these authors showed that the amount of EMG activity was about 40% greater for slow movements against a load than for isometric contractions against the same load in all elbow flexor muscles. This finding was later corroborated by van Bolhuis and Gielen (1997). The larger EMG activity could not be explained by the force-velocity relationship since movement velocity was rather low. As a consequence the larger amount of EMG activity during movements was attributed to variations in the recruitment and firing rate behavior of MUs within a muscle.

Evidence for changes in the relative activation of MUs within a single muscle was presented by Nardone et al. (1989), who reported a reversal of recruitment order of MUs in triceps muscle surae during the lengthening phase of voluntary ankle rotations against an external load. Later, Howell et al. (1995) also found a reversal of recruitment order of MUs in the first dorsal interosseous muscle during voluntary concentric/eccentric movements of the

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index finger. If similar changes in recruitment order occur in other types of muscle contractions as well, these variations in MU activation within a muscle might explain the increased amount of EMG activity reported for movements.

To gain a better insight into the activity of MUs during isometric contractions and movements, we have recorded the action potentials (APs) of single MUs of the biceps brachii and brachialis muscles during sinusoidally modulated isometric contractions of the elbow in flexion direction and for sinusoidal flexion/extension movements of the forearm against an extension preload. Both the timing of the APs with respect to the force or position signal and the firing rate during the bursts of APs were analyzed.

## Methods

The experimental procedures used in this study have been approved by the medical/ethics committee of the University of Nijmegen and were set up in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects tested gave their informed consent prior to each experiment. None of the subjects had any known history of neurological or musculoskeletal disorder.

### Experimental set-up

Subjects were comfortably seated in a chair with the upper arm in a position of  $0^\circ$  anteflexion. Both the upper arm and forearm were in a horizontal plane passing through the shoulder. The forearm was supported by a cloth sling which was suspended from the ceiling such that the arm could be relaxed in a horizontal position (Fig. 1). The shoulder was strapped to the back of the chair to minimize movement of the shoulder. In some experiments the position of the shoulder was measured with an Optotrak system. This revealed that any movements of the shoulder were always smaller than 1.5 mm.

A lightweight aluminum bracelet was fixed around the wrist of the subject just proximal to the wrist joint. The bracelet was made to fit tightly but comfortably by forming a mold of elastic dental compound between the bracelet and the subject's wrist. A special mold was made for each subject. A cable was attached to the bracelet via a yoke and also to a torque motor which could provide a preload at the wrist in extension direction. The position of the wrist was measured by a potentiometer, with a resolution of 0.08 cm, connected to the torque motor. The cable passed through several pulleys on a metal arm which was positioned orthogonal to the forearm (Fig. 1). A strain gauge was incorporated between the cable and the yoke to measure force at the wrist in the flexion direction with an accuracy of 0.1 N. Both the position and force signal were sampled at 500 Hz.

### MU recording

MU activity was recorded in the brachialis and biceps brachii (caput breve) muscles with intramuscular fine-wire electrodes at a sample rate of 16 kHz. Bipolar recordings of single MU activity were obtained using nylon-coated, 25  $\mu$ m diameter wires (material: Karma, Californian Fine Wire Co.) inserted into the muscle with a hypodermic needle. Two sterilized needles were inserted in each muscle with four wires in each needle. For each needle bipolar recordings were obtained by selecting the combination of the two wires which gave the best recordings. After amplification and band-pass filtering from 0.3 to 5 kHz, single MU APs were discriminated from the intramuscular EMG signals with a commercially available Brainwave system using any of several criteria, such as template matches and principal components. Typically the APs of two or three MUs could reliably be recorded and discriminated in each pair of electrodes. We

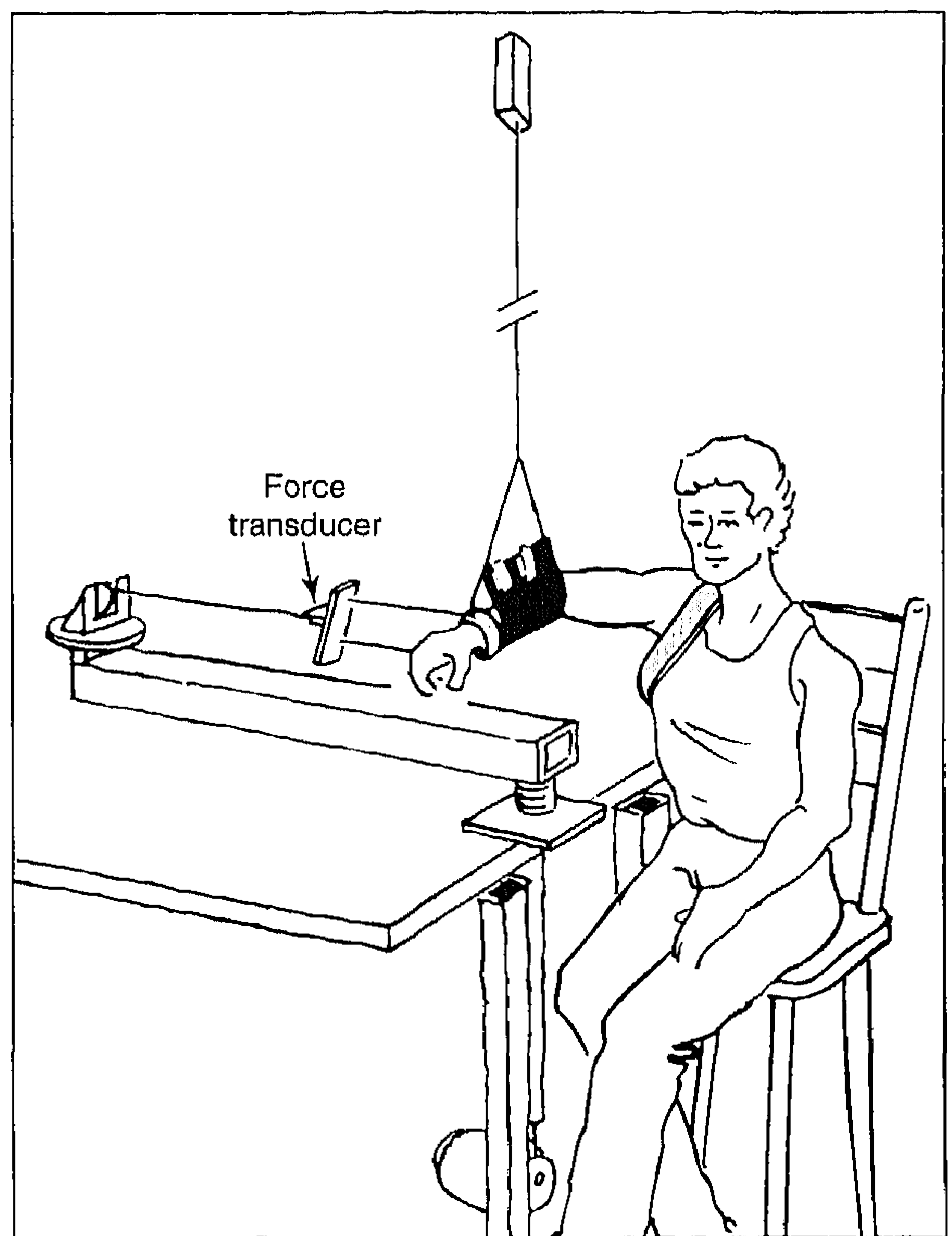


Fig. 1 Schematic overview of the experimental set-up

monitored the discrimination process carefully, both during the experiment and during the data analysis, to ensure that all APs detected belonged to a particular MU. We verified that any changes in shape of the APs of the MUs (especially during movements) were small and gradual. Also the IRTs of the MUs were recorded before and after the experiment. Comparing these results ensured that the same MUs were traced over the entire experiment. Since the duration of an AP (approximately 2 ms or shorter) is much smaller than the interspike interval (approximately 40 ms or longer), the possibility of not recording an AP due to interference with APs of other units was small. Detailed analysis revealed that interference of APs could have given rise to a reduction in the number of APs recorded by less than 3%.

### Experimental protocol

First MU activity was measured in isometric conditions, in which the horizontal force produced at the wrist was displayed on an X/Y oscilloscope in front of the subject. For the isometric condition the cable was fixated so that no movement of the elbow in the flexion direction was possible. The subject was asked to increase and decrease the isometric flexion torque in the elbow so as to track a sinusoidally varying target signal on the oscilloscope. The amplitude of the target signal was set such that isometric force at the wrist varied sinusoidally from 0 to 30 N [corresponding to 10–20% of the maximum voluntary contraction (MVC), depending on the subject] at typically nine different frequencies evenly distributed between 0.02 and 4.1 Hz.

Subsequently, the fixation of the cable was removed and the position of the wrist was displayed on the oscilloscope. In this condition the subject was instructed to track a sinusoidal target signal by flexion/extension movements in the elbow joint with an approximately constant amplitude (peak-peak amplitude about  $30^\circ$  centered at the isometric test position). Subjects were tested at typically nine different frequencies evenly distributed between 0.05 and 2.4 Hz.



These movements were made against various preloads in extension direction applied to the wrist by the torque motor. The force at the wrist, measured by the strain gauge, was fed back to the torque motor in order to minimize variations in preload at the wrist due to friction and inertia in the experimental set-up. Any variations in preload were reduced to values below 15% of the preload in this way. The muscle force was therefore the sum of a force counteracting the preload and a frequency-dependent periodic force term to overcome the stiffness, viscosity and inertia of the forearm. Due to the extension preload no active muscle force in extension direction was needed to move the arm in extension direction during the sinusoidal movements. Therefore only the elbow flexor muscles had to produce force. This was verified in several experiments by means of surface EMG recordings of the three heads of the triceps muscle, which did not reveal any EMG activity. All frequencies were tested for several values of the constant preload. The range of preloads was not constant since it depended on the recruitment threshold of the MUs under study.

#### Data base

Eleven subjects, ranging in age between 24 and 42 years, were tested in 12 experiments. In total the activity of 57 MUs was recorded. For 44 MUs the firing behavior was recorded for the isometric as well as for the movement task for all frequencies. For three MUs (one experiment) the activity was recorded only during the isometric task for all frequencies and for ten MUs (four experiments) the activity was recorded for a frequency of 0.02 Hz during the isometric task and for all frequencies during the movement task.

#### Data analysis

The temporal relation between APs, force and position of the wrist was investigated using a cross-correlation function. The sequence of APs was represented as a point process with a time resolution of 1 ms. The mean difference in time,  $\tau$ , between the APs on the one hand and force or position on the other hand was determined by the time of the peak of the normalized cross-correlation function. The normalized cross-correlation function between two signals  $x(t)$  and  $y(t)$  is defined as

$$\Phi_{xy}(\tau) = \left\{ (2T)^{-1} \int_{-T}^T x(t+\tau) y(t) dt \right\} / \left\{ \sqrt{(2T)^{-1} \int_{-T}^T x^2(t) dt} \cdot \sqrt{(2T)^{-1} \int_{-T}^T y^2(t) dt} \right\}.$$

The time delay,  $\tau$ , depended on the timing of recruitment and de-recruitment of the MU with respect to the force or position signal as well as on the modulation of the firing rate during the period that the MU was recruited. However, since the modulation of the firing rate was more or less symmetric over the period that the MU was active, the time delay was mainly determined by the timing of (de- and) recruitment with respect to the force or position signal.

Each trial (i.e., a set of isometric contractions or movements at a particular frequency) typically contained 5–15 cycles (depending on the movement frequency). To obtain an estimate of the error in the time delay between APs and force/position, the time delay was determined twice in repeated trials. If the data were be completely reproducible, the time delay in the second trial plotted against the time delay in the first trial should fall on a straight line with slope 1 for all frequencies. By calculating the mean scatter, defined as the square root of the mean of squared distances of the points relative to the line  $y=x$ , an estimate of the standard deviation in the time difference could be obtained. This procedure is equivalent to determining the variance in a set of paired trials (Snedecor and Cochran 1980).

Some MUs revealed alternately only a few or no APs during some trials. This was particularly found for MU's with a high IRT, which were not active during movements at low frequencies. Presumably, the forces related to slow movements were not large enough to recruit MU's with a high IRT. Other MUs, in particular those with a relatively low IRT, revealed an almost constant firing rate at a high level during some trials. The phase lead of these MUs, calculated for these trials, was therefore meaningless. For these MUs the data in these trials was not taken into consideration.

The firing rate of a MU at a time  $t$  was defined as the number of spikes in an interval of 200 ms centered around time  $t$  divided by 200 ms. The mean firing rate in a sinusoidal period was defined as the number of APs averaged over a number of periods (ranging from 5 to 15) divided by the duration of the period. To fit the phase relation of MU activity for isometric contractions at various frequencies a second-order linear low-pass system was used. The low-pass system was characterized by the impulse response  $h(t)=t \exp(-t/T)$ , which in the frequency domain is represented by the transfer function  $H(\omega)=1/(1+i\omega\tau)^2$ , where  $\tau$  is a time constant. The phase relation between input and output signals of this system is given by  $\Phi(\omega)=\arctan(-2\omega\tau/(1-\omega^2\tau^2))$ .

#### Results

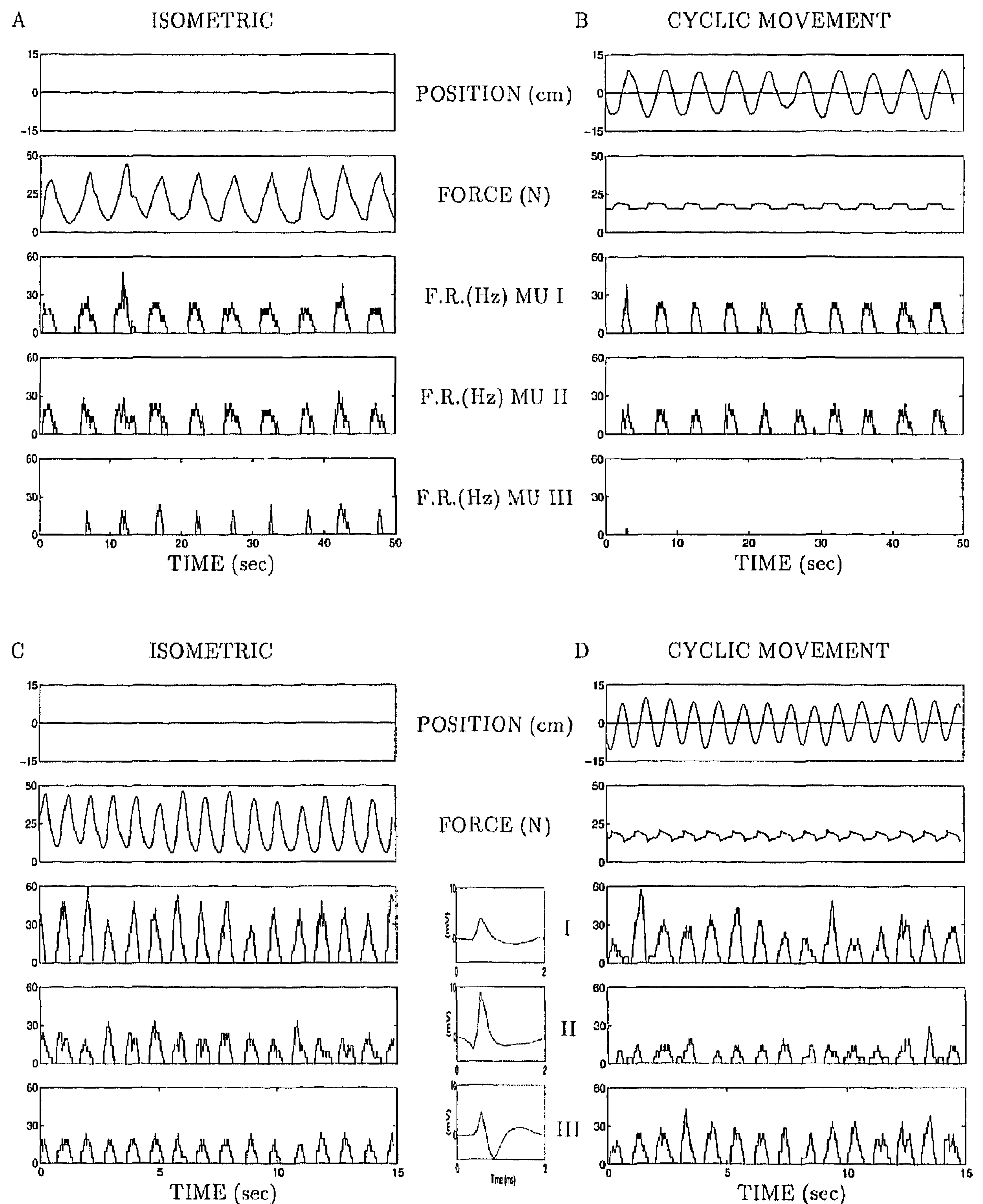
Figure 2 shows the firing pattern for three simultaneously recorded MUs (I, II and III) of the brachialis muscle of subject PH for isometric contractions (Fig. 2A,C) and for movements (Fig. 2B,D) for frequencies of 0.2 Hz (Fig. 2A,B) and 1.0 Hz (Fig. 2C,D). The top trace in each part of the figure shows the position of the wrist in centimeters. Flexion of the elbow caused a movement of the wrist in the positive direction. The second panel in each part of the figure shows the force at the wrist in flexion direction. The lower three panels of each part of the figure show the firing rates of the three MUs (I, II and III). The shape of the APs of the three MUs is plotted between the lower three panels of Fig. 2C and D. The IRTs of the MUs I, II and III are 20, 24 and 37 N, respectively.

For movements there is a small modulation of force at the wrist (see the force trace in Fig. 2B and D). This modulation is due to incomplete force feedback and to phase delays in the feedback loop. These modulations in force are typically 15% of the preload or less. In none of our data could we detect any abrupt changes in MU firing related to these small variations in force.

Figure 2 shows that the MUs are active in short, approximately symmetric bursts. For the isometric contractions at 0.2 and 1.0 Hz (Fig. 2A,C) the centers of the bursts of activity coincide for all MUs and, therefore, all three MUs have approximately the same temporal relationship. The mean time delay between the bursts of activity and the force is approximately 210 ms for the 0.2-Hz isometric contractions (Fig. 2A) and approximately 170 ms for the 1.0-Hz isometric contractions (Fig. 2C). These time delays correspond to phase shifts of 15° and 60°, respectively. For the low-frequency movement (Fig. 2B) MU III, which has the highest IRT, was not active. At the higher movement frequency (Fig. 2D) all three MUs were active and their bursts of activity had approximately the same phase relation relative to the position trace. Note, however, that the firing rate of MU II is smaller than that of MU III for movements at 1.0 Hz.



**Fig. 2** An example of the firing behavior (*F.R.* firing rate) of three simultaneously recorded motor units (MUs) in the brachialis muscle of subject PH for sinusoidally modulated isometric contractions (**A**, **C**) and for sinusoidal movements (**B**, **D**) at 0.2 Hz (**A** and **B**) and 1 Hz (**C**, **D**). The shape of the corresponding action potentials of the three MUs is plotted between the firing rate panels of **C** and **D**. The *top two signals* in each panel show the position (flexion in positive direction) and flexion force in the elbow, respectively. Position zero corresponds to an elbow angle of  $90^\circ$



On the contrary, MU III is not active at all at 0.2 Hz movements, while MU II reveals a firing rate which exceeds that at 1.0 Hz. This indicates that the firing rate of MUs changes in a complicated way with movement frequency. This will be discussed in more detail later.

The results shown in Fig. 2 illustrate a result typical for the majority of MUs. However, in a considerable number of experiments different results were found. All these results will be presented in two parts. First we will focus on the phase relation of MU activity relative to force (in isometric contractions) or position (for movements) and, subsequently, on the modulation of firing rate during sinusoidal isometric contractions and movements.

#### Phase relation

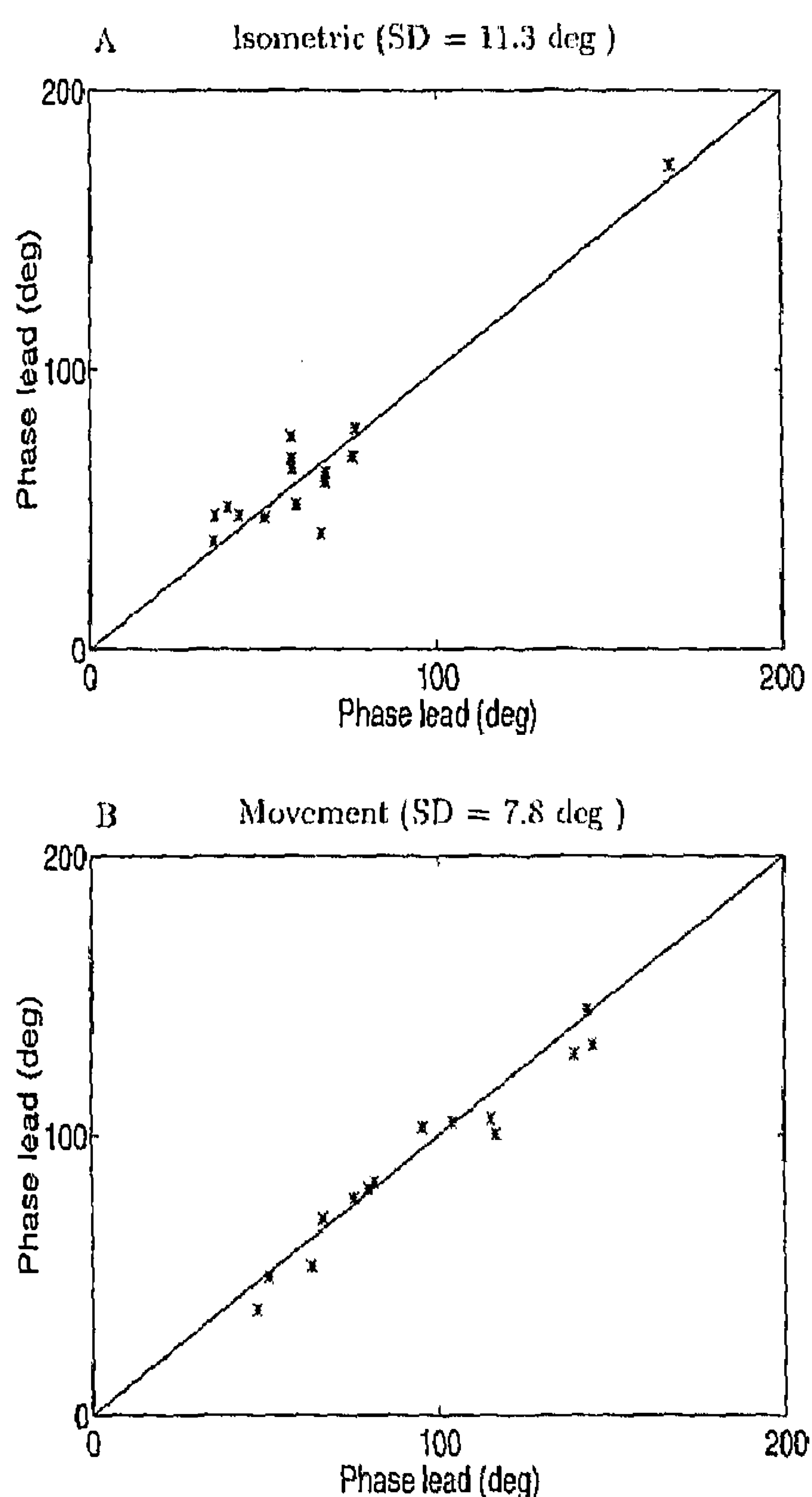
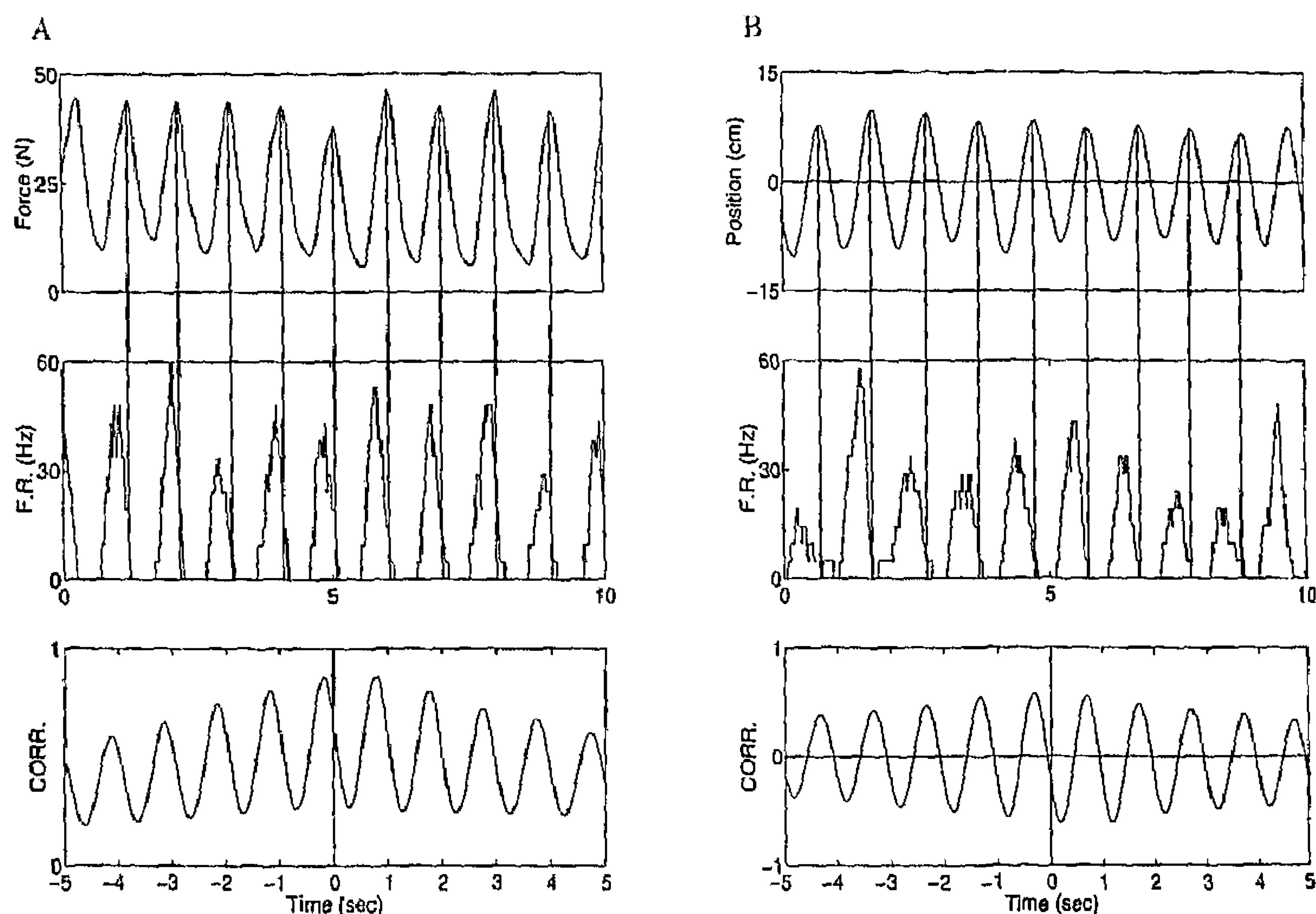
An estimate of the mean phase lead of the bursts of APs of a MU relative to force or position was obtained from

the cross-correlation function between the APs and the force or position signal. An example is shown in Fig. 3.

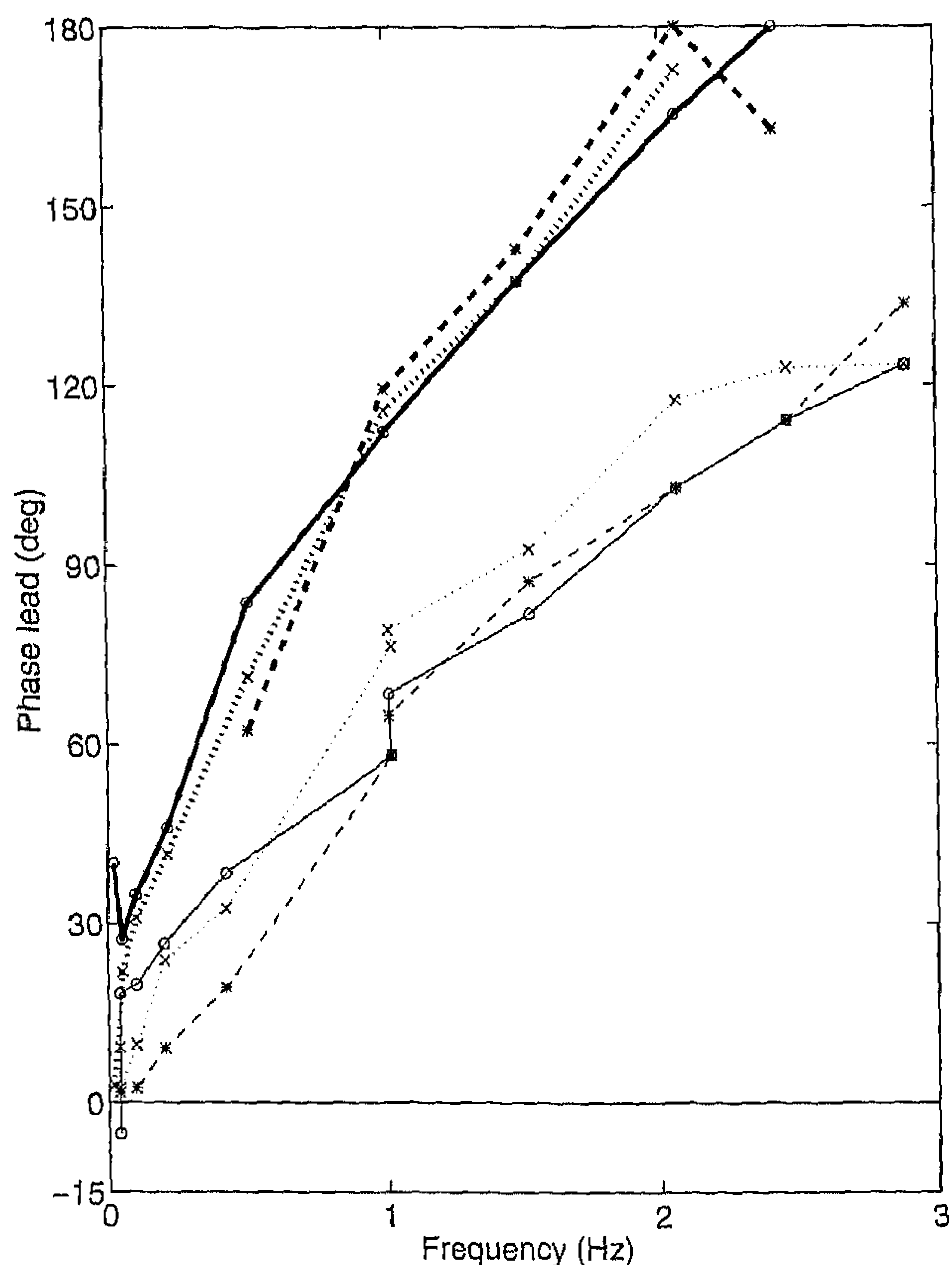
Figure 3A and B show the firing rate of MU I for the same trials as shown in Fig. 2C and D, respectively. A mean value for the phase difference between the bursts of APs and the force (Fig. 3A) or position (Fig. 3B) signal was obtained by calculating the time of the peak of the cross-correlation function. This phase lead is mainly determined by the timing of recruitment and decruitment of the MU with respect to the force or position signal. The shape of the bursts plays only a minor role in determining the mean phase lead of the bursts, since the bursts of APs are more or less symmetric.

Figure 3A shows that the bursts of activity lead the force signal by 167 ms, corresponding to a phase lead of  $60^\circ$ . For movements at the same frequency the APs lead the position signal by 313 ms, corresponding to a phase lead of  $113^\circ$  (Fig. 3B). For all MUs the phase lead

**Fig. 3** The *top traces* show the isometric force signal (**A**) and the position signal (**B**). The *middle panels* of **A** and **B** show the firing rate of MU I, and the *bottom panels* of each part of the figure show the normalized cross-correlation functions of the two corresponding signals plotted above. *Vertical lines* have been drawn at the peaks of the force and the position signal in order to illustrate the phase lead of the bursts in each cycle



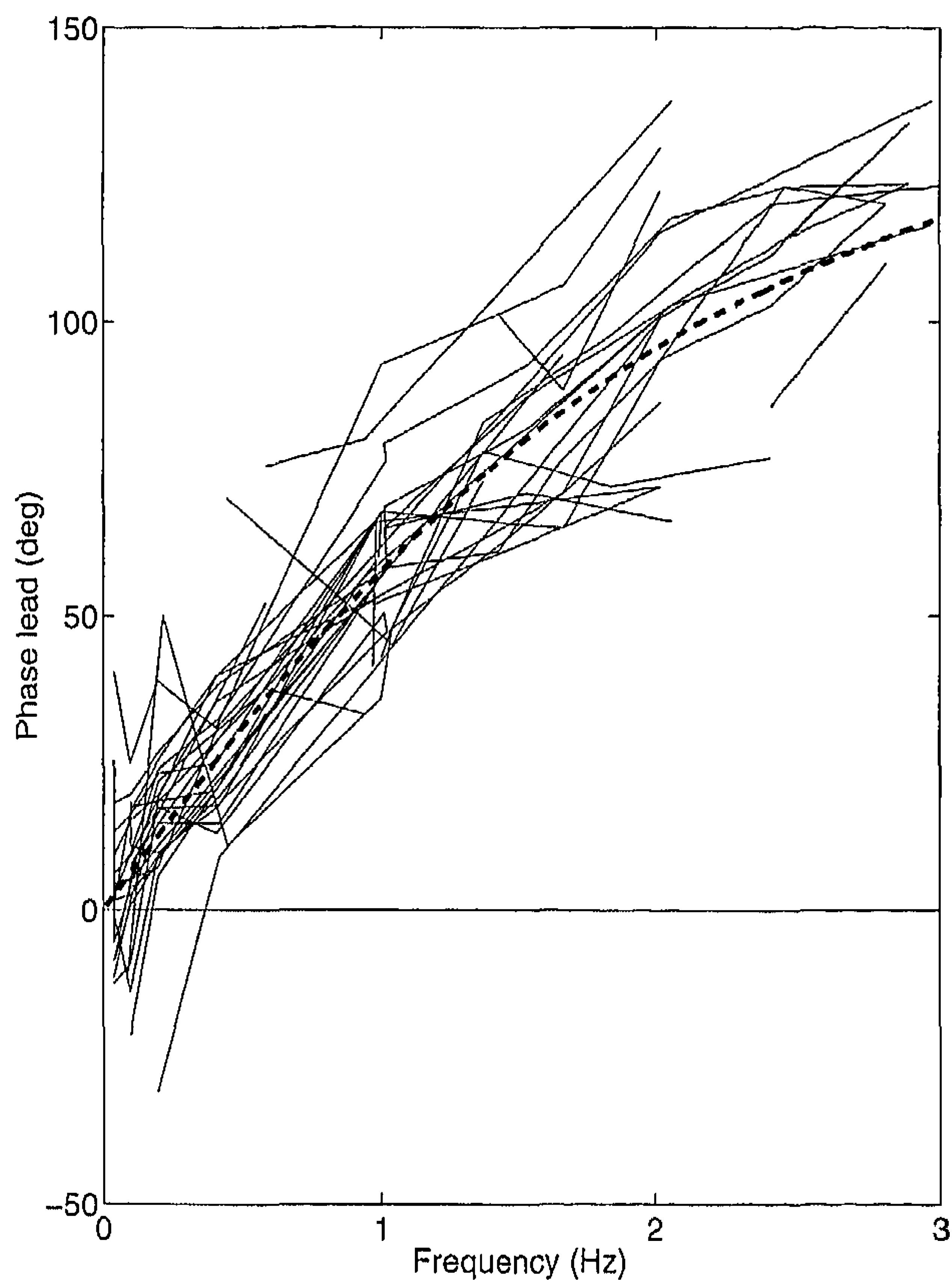
**Fig. 4** **A** The phase lead for 17 repeated isometric trials. (Some data points coincide.) The phase lead of the first trial is plotted on the *horizontal axis* and that of the corresponding second repeated trial on the *vertical axis*. By calculating the mean scatter, defined as the square root of the mean of squared distances of the points relative to the line  $y=x$  (*continuous line*), an estimate of the standard deviation in the phase lead could be obtained. **B** The phase lead for all 14 repeated movement trials



**Fig. 5** The phase lead of the bursts of action potentials (APs) to the force or position signal as a function of frequency for the three MUs I (*circles and continuous lines*), II (*crosses and dotted lines*) and III (*asterisks and dashed lines*) for both the isometric (*thin lines*) and the movement conditions (*thick lines*)

for movements exceeded that for isometric contractions for all frequencies. This will be discussed in more detail later. An estimate of the error in the value of the phase lead was obtained by repeating several trials for various frequencies and calculating the phase lead for each of

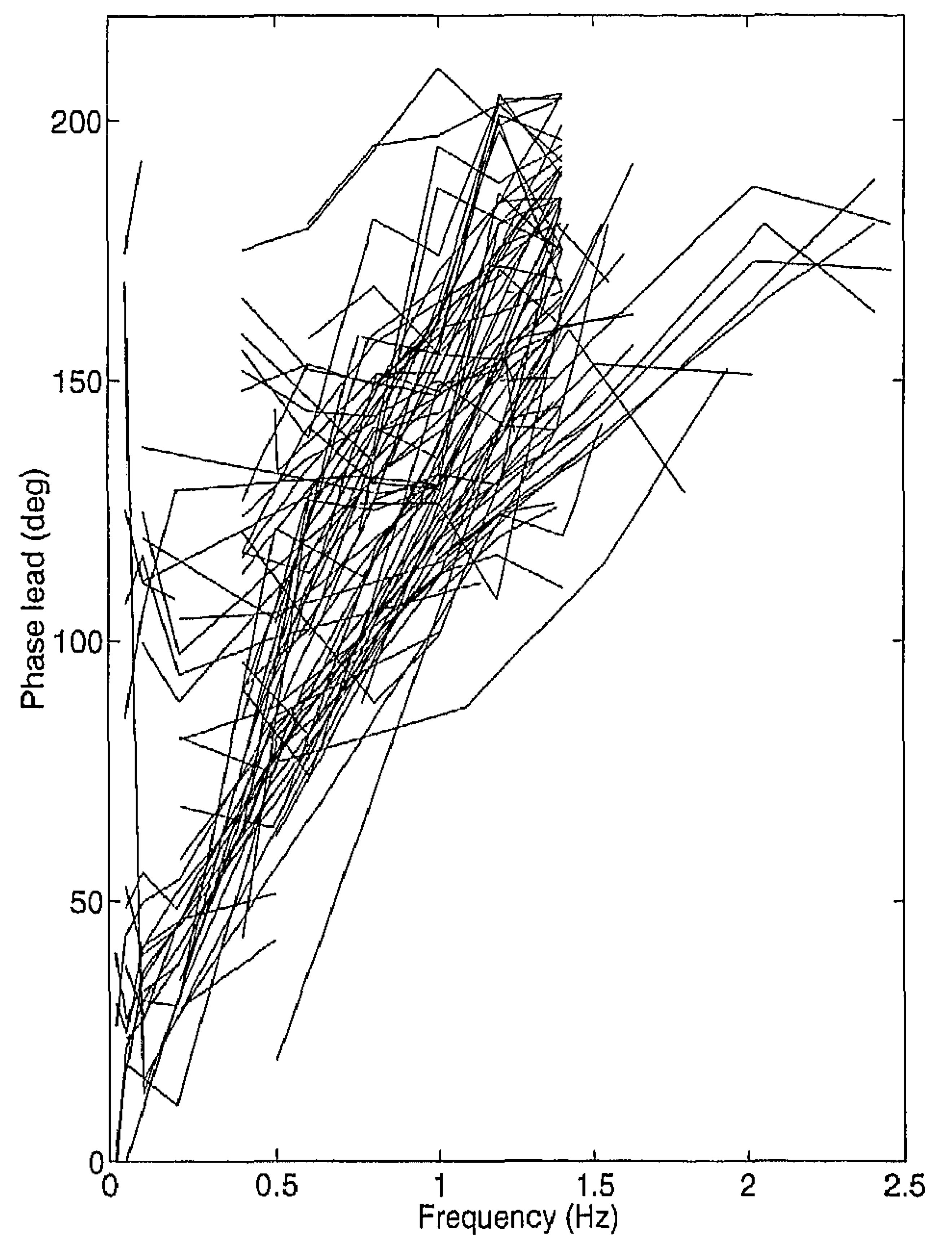




**Fig. 6** The mean phase lead of the bursts of APs with respect to the sinusoidal modulations in isometric force (range 0–30 N) in the flexion direction at the wrist for all MUs recorded isometrically (39) as a function of the contraction frequency. The *thick dashed line* shows the phase lead of a second-order low-pass system with a time constant of  $\tau=89$  ms, which is the mean of the time constants of the second-order systems fitted to the phase leads of the individual MUs

these trials. In Fig. 4A and B the phase lead of APs relative to the force or position signal for all repeated trials is plotted for the isometric and the movement task, respectively. For the isometric task the standard deviation was  $11.3^\circ$ ; it was  $7.8^\circ$  for the movement trials. These results provide a measure of the accuracy of the estimates for the phase relation of the MUs.

Figure 5 shows the mean phase leads of the bursts of APs to the force or position signal plotted as a function of frequency for the same three MUs (I, II and III) as shown in Fig. 2, for the isometric task (thin lines) and the movement task (thick lines). In both tasks the phase lead increases with frequency, but the increase is steeper for the movement task. Note that the phase relation is very similar for all three MUs. MU III, with the highest IRT, is not active for movements at frequencies below 0.5 Hz. In all other aspects all three MUs behave in much the same way. First we will focus in more detail on the isometric phase relations and then on the phase relations of the MUs during movements.



**Fig. 7** The mean phase lead of the bursts of APs relative to the position of the wrist as a function of movement frequency for all MUs (45) recorded during the movement task for all subjects

### Isometric phase relation

To quantify the phase relation of MU activity with isometric force at the hand for various frequencies we have fitted a second-order linear low-pass system (see Methods) to the phase relation between the APs and the isometric force at the wrist.

Figure 6 shows the mean phase leads of the bursts of APs with respect to the force at the wrist for all MUs ( $n=39$ ), which were recruited during the isometric sinusoidal force modulations, as a function of the frequency. Fitting a second-order low-pass system (thick dotted line) to these phase relations by minimizing the sum of squared distances for all frequencies resulted in a mean time constant of 89 ms with a standard deviation of 39 ms.

### Movement phase relation

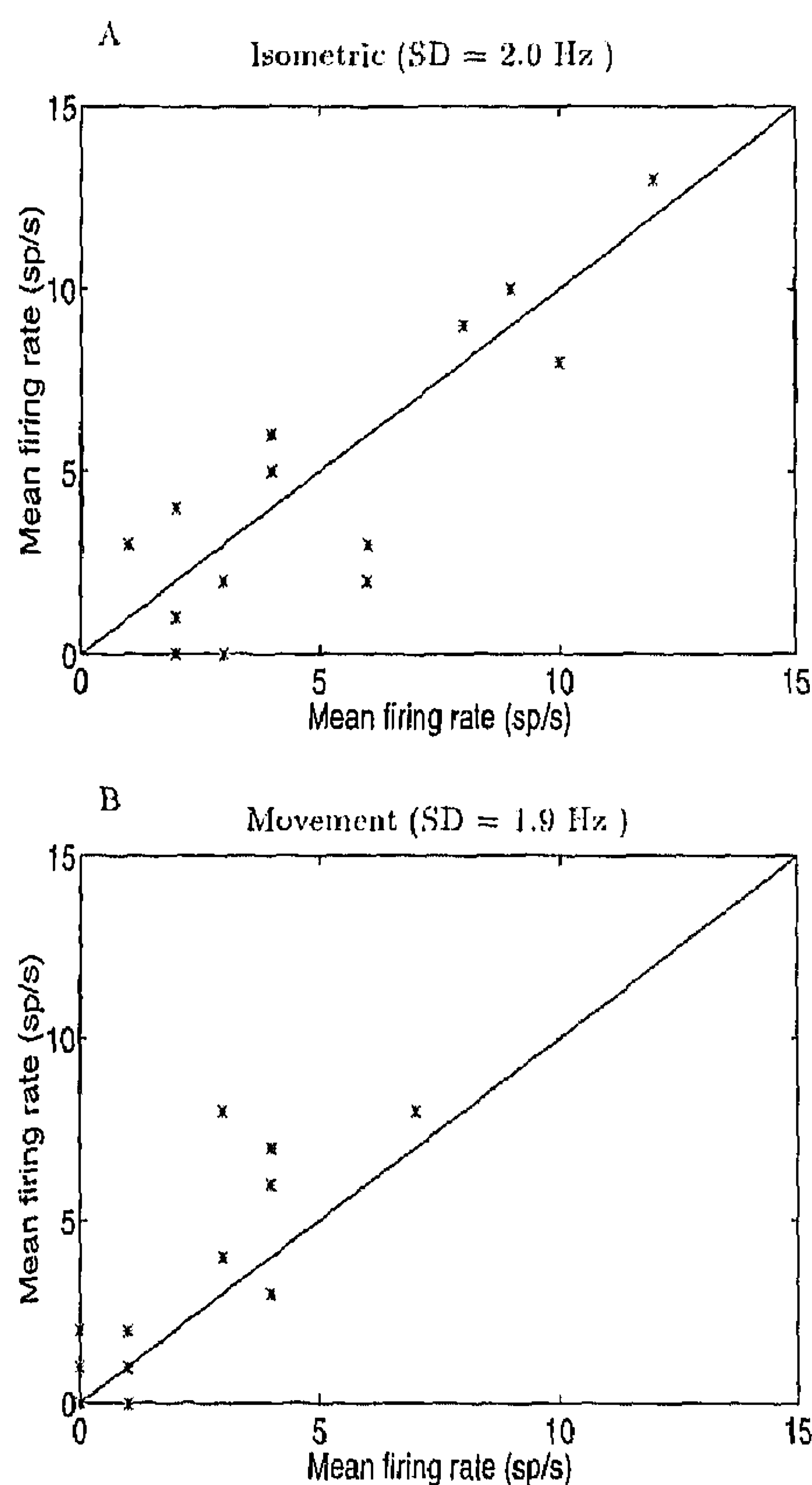
In Fig. 7 we have plotted the mean phase lead of the bursts of APs relative to the position signal as a function of movement frequency for all 45 MUs recorded. In general the phase lead increases gradually for all MUs. However, it is striking that the variability in phase lead be-

**Table 1** Statistical values

Frequency (Hz)	Slope (SD) (deg/N)	Intercept (SD) (deg)	Number of trials	$R^2$	Student $t$ value for slope	Two-tailed significance level for slope
0.50	0.71 (0.32)	67.3 (7.6)	36	0.13	2.21	0.034
0.78	0.45 (0.20)	120.3 (6.5)	51	0.10	2.31	0.025
1.00	0.44 (0.19)	127.5 (5.6)	78	0.07	2.34	0.022
1.20	0.42 (0.22)	149.6 (7.3)	54	0.07	1.91	0.062
1.45	0.26 (0.17)	161.2 (5.4)	70	0.03	1.50	0.139

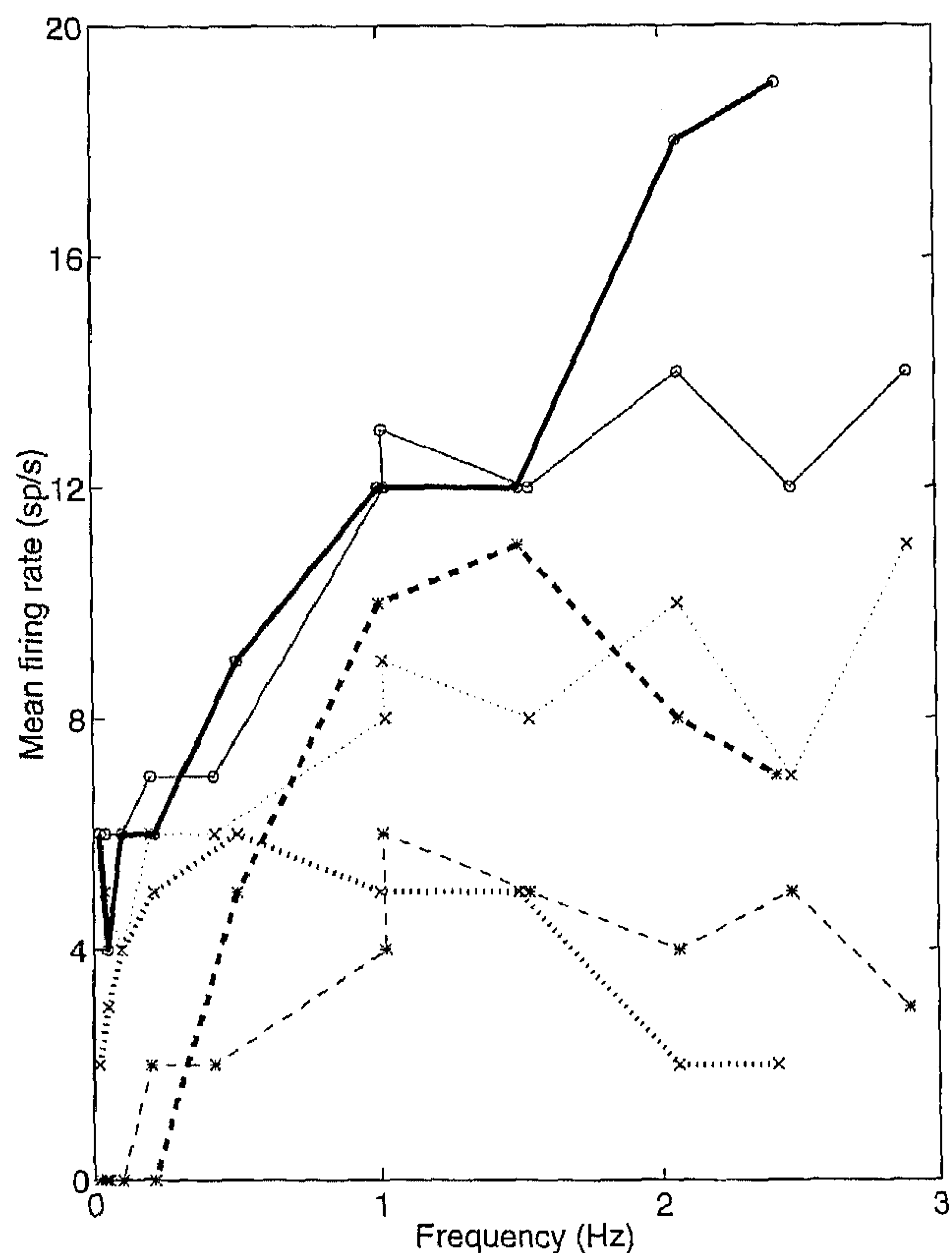
Statistical results of a linear regression fitted to the mean phase leads of the bursts of activity relative to the position of the wrist as a function of the isometric recruitment threshold (IRT) for various movement frequencies (first column). The second and third columns show the slope and the intercept value (with their corresponding standard

deviations) of the regression line, respectively. The fourth column shows the number of trials used in the calculations. The fifth column shows the  $R^2$  value of the fit and the sixth and seventh column show the Student's  $t$ -test value and the corresponding two-tailed significance level, respectively



**Fig. 8 A, B** Mean firing rate for all 17 repeated isometric trials and the 14 repeated movement trials, respectively. (Some data points coincide.) By calculating the mean scatter, defined as the square root of the mean of squared distances of the points relative to the line  $y=x$  (continuous line), an estimate of the standard deviation in the phase lead is obtained

tween MUs is much larger than for the isometric case. Recall that the standard deviation in the phase lead for movement trials was only  $7.8^\circ$ , which was smaller than that for isometric trials. This demonstrates that the large variability in Fig. 7 is not caused by a variability in the phase lead of each individual MU, but rather it reflects a variability in phase lead between MUs. The same variability was found for MUs in the brachialis and biceps muscles, excluding an effect of muscle specificity. Cor-

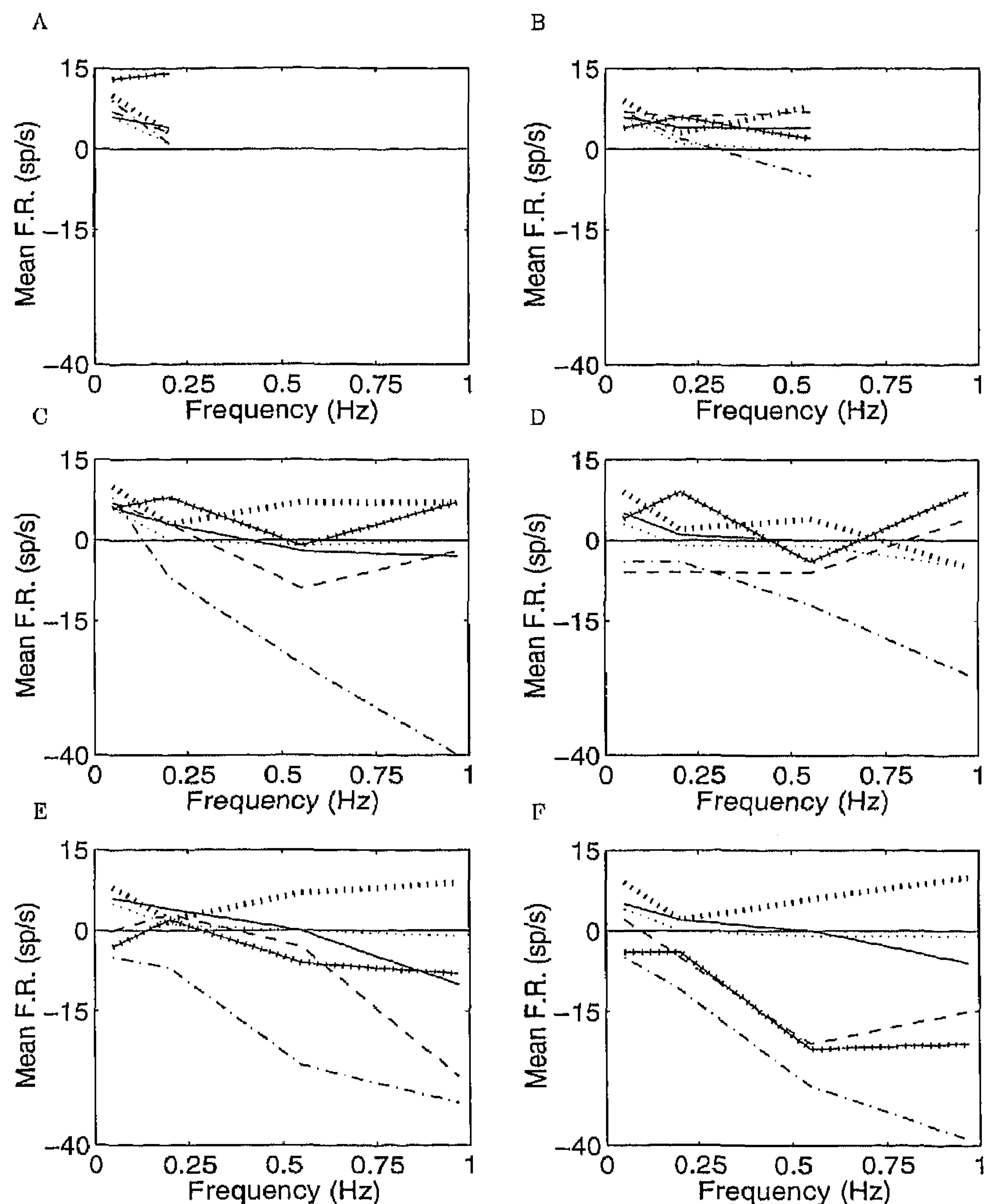


**Fig. 9** The mean firing rate for the three MUs I (circles and continuous lines), II (crosses and dotted lines) and III (asterisks and dashed lines) for the isometric task (thin lines) and the movement task (thick lines) as a function of frequency

relating the phase lead of the MUs during movements with the IRT revealed a small correlation between IRT and phase lead (Table 1), in such a way that MUs with a high IRT tend to be activated with larger phase leads, whereas MUs with a low IRT tend to be activated with smaller phase leads. Table 1 shows that the slope of the linear regression deviates significantly from zero for the lower movement frequencies. However, this table also shows that the correlation coefficient is rather small,



**Fig. 10A–F** Difference in mean firing rate in the isometric contractions relative to that for movements as a function of frequency. In A–F the preload in extension direction during the movements was 3.9, 5.8, 9.2, 11.4, 16.7 and 21.7 N, respectively. All these MUs were recorded simultaneously



indicating that the IRT explains only a small part of the variance.

### Firing rate

The mean firing rate during a burst of APs was calculated by counting all the APs over a certain number of periods (ranging from 5 to 15) and dividing this number by the number of periods and the duration of each period. An indication of the error in the calculated value of the mean firing rate was obtained by repeating this procedure for several trials. Figure 8 shows the data obtained in the repeated trials. The same repeated trials were used as for the calculation of the standard deviation of the phase lead. The standard deviation in the mean firing rate was estimated in the same way as was done for the phase relations. It appeared to be 2.0 spikes/s for the isometric task and 1.9 spikes/s for the movement task.

Figure 9 shows the mean firing rate for the same three MUs (I, II and III) as shown in Figs. 2 and 5, as a function of frequency for the isometric task (thin lines) and the movement task (thick lines). The mean firing rate increases with frequency both for isometric contractions and for movements. Figure 9 shows that the mean firing rate of

MU I is approximately the same for the isometric task and for the movement task for most frequencies. For MU II, however, the mean firing rate is much smaller and for MU III it is much higher in the isometric task than in the movement task. This illustrates that there exists a variable firing rate behavior for the isometric task relative to the movement task for different MUs. This variability becomes even more pronounced in Fig. 10.

Figure 10 shows the difference in mean firing rate in each period in the isometric task relative to that in the movement task as a function of frequency for six MUs (five in the biceps and one in the brachialis muscle). All these MUs were recorded simultaneously from subject VC. Figure 10A–F show data obtained in movement trials against preloads of 3.9, 5.8, 9.2, 11.4, 16.7 and 21.7 N, respectively. The data of the movement trials shown in Fig. 10A–F were all compared with the same isometric trials. A positive value in Fig. 10 means that the mean firing rate was larger for the isometric trial than for the movement trial at that frequency. For small preloads high-frequency movements could not be tested since then activation of extensor muscles became apparent, which was not in line with the experimental protocol. The firing behavior of the MUs in Fig. 10 is typical for all subjects.

Figure 10A–F demonstrate a tendency for lower firing rates for isometric contractions than for movements at higher frequencies. Since the acceleration of the arm increases with increasing frequency for movement trials, the peak forces exerted by the flexor muscles also increase with frequency. Thus for movement trials the mean force level exerted by the flexor muscles increases with frequency, whereas the mean force level during isometric trials remains the same for all frequencies. This may explain the decrease in the firing rate difference with frequency. However, note that the various MUs, which have been recorded simultaneously, have a different frequency-dependent behavior. Moreover, Fig. 10 shows that overall the differences of the mean firing rate show a small decrease for increasing preloads (Fig. 10A–F). This has to be expected since the mean force at the wrist increases with preload and therefore also the mean firing rate during the movement trials.

What is remarkable is the fact that the firing rate behavior is significantly different for different MUs. Note that the standard deviation in each of the data points is approximately 2 spikes/s, which makes the behavior of different MUs significantly different. The differences in firing rate for various MUs indicate that the various MUs are activated differently in the isometric and the movement task. These differences become more pronounced for higher preloads, as can clearly be seen in Fig. 10F, which shows that some MUs are activated more during movement tasks than during isometric trials (negative values), whereas other MUs are activated more during isometric trials than during movement trials (positive values). MUs in the brachialis and biceps brachii muscles showed the same behavior. Note that the different firing behavior of MUs does not reflect variability in experimental conditions, since the different behavior of MUs in isometric trials and in movements was observed simultaneously for all MUs in Fig. 10.

## Discussion

The main result of this study is that different MUs in the same muscle reveal a different behavior for isometric contractions and for movements at different frequencies. These differences became apparent both in the phase relation of the APs relative to the force and position of the wrist (i.e., in the timing of recruitment and decruitment) and in the modulation of the firing rate of the MUs at different frequencies and preloads. We will discuss these differences separately.

### Isometric phase relation

We have seen that the mean phase lead of the bursts of APs relative to the isometric force at the wrist gradually increases with contraction frequency in a similar way for all MUs. The phase relations could be fitted well by a second-order linear low-pass system with a mean time constant of 89 ms.

Assuming that the force twitch of a MU can be described by a second-order linear low-pass system, former studies (ter Haar Romeny et al. 1984) have obtained values for the time constant of the force twitch of MUs in the biceps brachii near 50 ms. However, a MU contributes to sinusoidal contractions with a sequence of APs, not with a single AP. The non-linear summation of the force twitches of a MU (see, e.g., Koehler et al. 1984; Powers and Binder 1991) will effectively enlarge the time constant of the linear approximation of the force pulse produced by the MU. Therefore, the mean value of the time constant found in this study,  $\tau=89$  ms, is well within the range which may be expected if the phase behavior for isometric contractions is thought to be attributed mainly to the MU twitches.

### Movement phase relation

For the phase relation of MUs during movements a different picture was observed. The overall increase in the mean phase lead of the bursts of activity relative to the position of the wrist with movement frequency appeared to be steeper than the increase in the mean phase lead observed during the isometric task. Since the forearm can be described by a second-order low-pass system (Kearney and Hunter 1990), a progressive phase lead of the force produced at the wrist with respect to the position of the wrist has to be expected for increasing movement frequency. Therefore, an increase in the phase lead of MU activity relative to the position during movement trials which is steeper than that relative to the force during the isometric trials has to be expected for increasing movement frequency. The results shown in Fig. 5 are therefore in line with theoretical predictions.

Whereas Fig. 6 demonstrates that all MUs show more or less the same phase relations during the isometric contractions, Fig. 7 reveals that there exists a large variability in phase relations of the MUs during the movements. Since the phase lead of MUs could be determined accurately ( $SD=7.8^\circ$ ), this variability could not be explained by the error in the method of obtaining the mean phase lead. It therefore means that different MUs show a different change in phase relation when shifting from isometric tasks to movements.

### Firing rate behavior

Figures 9 and 10 show that the firing-rate behavior of different MUs in the same muscle is different for movements and for isometric contractions. Some MUs have higher firing rates during movements whereas others have higher firing rates during the isometric tasks. These large differences show that some MUs (those with a negative difference in Fig. 10) contribute more to movements, whereas other MUs (those with a positive difference in Fig. 10) contribute more to isometric contractions. Therefore, the firing-rate behavior of the MUs underlines the result ob-



tained from the phase relations of the MUs, regarding a different relative activation of the MUs for movement tasks and isometric tasks.

### MU recording

Recording of MU activity has always been difficult due to possible movement artifacts. We are convinced, however, that the findings described in this paper (i.e., a different relative activation of the MUs for isometric tasks and movements) cannot be attributed to movement artifacts. We have carefully checked the shape of APs throughout the recording, as well as during the analysis with the Brainwave system, which characterizes each AP by a series of parameters. In case of doubt the recording was discarded from further analysis. Therefore, we were sure that all APs grouped together belonged to the same MU. As mentioned in Methods the possible loss of the recording of APs due to interference with APs of other MUs was small (less than 3% loss of units), since the duration of an AP is much smaller than the inter-spike interval (even at the highest firing rate). The large differences in firing rate (Fig. 10) and the different timing of recruitment (Fig. 5) observed between tasks can therefore not have been the result of losing some APs. In addition, it is highly unlikely that movement artifacts could give rise to the consistent results in this study.

At those points where our results can be compared with previous studies our findings are in line with these earlier results or with theoretical expectations. For example, all MUs show more or less the same phase relation during the isometric contractions corresponding to a time constant of 89 ms, which is in line with earlier findings. For movements, the increase in the mean phase lead of the bursts is steeper than that for the isometric contractions, which is in line with theoretical expectations. Also the variability in the phase lead and in mean firing rate appears to be smaller during movements than during isometric contractions, which is just the opposite of what would be expected, since movement artifacts in MU recordings are most prominent during movements.

### Selective activation of MUs

The results in this study convincingly demonstrate a different activation of the MU population in a muscle for isometric contractions and for movements. These results extend previous reports on a different activation of MUs of various muscles during natural sinusoidal tasks (Smith et al. 1980) and reports on a different activation of MUs of various muscles in isometric contractions and movements (Tax et al. 1990; Theeuwen et al. 1994), in that the present study demonstrates differences *within* the population of MUs of a *single* muscle between the two tasks, indicating a task-dependent activation of the motoneuron pool of a single muscle.

Since different MUs have different contractile properties (Thomas et al. 1990; Cope and Clark 1991; Riek and

Bawa 1992) a reshuffling of recruitment among MUs may give rise to a different force output. Therefore, a different activation of the various MUs could give rise to a different force-EMG relationship. A larger amount of EMG activity for movements against the same force as in isometric contractions (Theeuwen et al. 1994; van Bolhuis and Gielen 1997) could have been obtained by having more MUs recruited at a lower firing rate (Solomonow et al. 1987). Our data did not reveal firm evidence for the fact that a larger number of MUs is recruited during movements. This was mainly due to the fact that it was hard to compare the muscle forces during isometric contractions with those during movements. In order to estimate muscle force during movements, first an accurate, detailed model of the human arm would be required to estimate elbow torque during movements, and secondly a reliable method of distributing elbow joint torque over the various elbow flexor muscles would be necessary. Since these procedures would have caused relatively large error bounds in the estimated muscle force we could not accurately compare recruitment thresholds of MUs in the isometric and movement conditions and, as a consequence, could not provide a good quantitative explanation for the larger amount of EMG activity during movements as reported by van Bolhuis and Gielen (1997) and by Theeuwen et al. (1994).

Correlating the phase lead of the MUs during movements with the IRT revealed for most contraction frequencies a small but significant correlation between IRT and phase lead in such a way that MUs with a high IRT tend to be activated with larger phase leads whereas MUs with a low IRT tend to be activated with smaller phase leads. Since in Fig. 7 a phase lead larger than  $180^\circ$  means that the MUs were mainly active in the lengthening phase of the movement, the correlation between IRT and phase lead mentioned above implies that, in general, the MUs with a relatively high IRT tend to be active in the lengthening phase, suggesting that these MUs are recruited in time before MUs with a lower IRT. Therefore, our data corroborate the findings of Nardone et al. (1989) and Howell et al. (1995) on reversal of recruitment order during the lengthening phase of voluntary rotations.

The question now arises regarding the extent to which these differences have to be attributed to differences in the activation of the MU population by the central nervous system, or whether the MU-specific differences have to be attributed to preferential input to MUs by various sensory afferents. Stephens et al. (1978) have shown that the firing rate of MUs in the first dorsal interosseous muscle, with a relatively low IRT, can be reduced by cutaneous stimulation during voluntary contraction, while the firing rate of MUs with a higher IRT remains unaffected. This supports the hypothesis of MU-specific afferent input. Other support for this hypothesis comes from studies which have shown a selective activation of MUs in triceps surae muscles of the cat after stimulation of the sural nerve (Burke et al. 1970; Kanda et al. 1977). Another possibility might be that central commands affect both  $\alpha$ - and  $\gamma$ -motoneurons such that changes in the activation of MUs



during movements result from direct central effects and from indirect effects originating from a different setting of  $\gamma$ -motoneurons. The present data do not allow us to distinguish between these hypotheses.

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